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Effects of background noise on acoustic characteristics of Bengalese finch songs

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Online regulation of vocalization in response to auditory feedback is one of the essential issues for vocal communication. One such audio-vocal interaction is the Lombard effect, an involuntary increase in vocal amplitude in response to the presence of background noise. Along with vocal amplitude, other acoustic characteristics, including fundamental frequency (F0), also change in some species. Bengalese finches (*Lonchura striata* var. *domestica*) are a suitable model for comparative, ethological, and neuroscientific studies on audio-vocal interaction because they require real-time auditory feedback of their own songs to maintain normal singing. Here, the changes in amplitude and F0 with a focus on the distinct song elements (i.e., notes) of Bengalese finches under noise presentation are demonstrated. To accurately analyze these acoustic characteristics, two different bandpass-filtered noises at two levels of sound intensity were used. The results confirmed that the Lombard effect occurs at the note level of Bengalese finch song. Further, individually specific modes of changes in F0 are shown. These behavioral changes suggested the vocal control mechanisms on which the auditory feedback is based have a predictable effect on amplitude, but complex spectral effects on individual note production. © 2016 Acoustical Society of America. [http://dx.doi.org/10.1121/1.4968577]

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I. INTRODUCTION

Many animals communicate by various acoustic signals. In particular, vocalization is one of the most widespread domains of communication among vertebrates (Nottebohm, 1972; Seyfarth *et al.*, 1980; Brumm and Slabbekoorn, 2005). Although there have been many comparative studies, the mechanism of vocalization is not completely understood (Jürgens, 2009). Additionally, some species are observed to have an audio-vocal interaction, meaning that auditory inputs can change their vocalization in real time (Kao *et al.*, 2005; Purcell and Munhall, 2006). To study vocalizations in certain species, it is necessary to investigate not only the acoustics of vocalization itself, but also the comprehensive behavioral and neural mechanisms interacting with the auditory system.

One example of such an audio-vocal interaction is the Lombard effect, an involuntary increase in vocal amplitude against the presence of background noise (Lombard, 1911). This effect has been studied in birds (Manabe *et al.*, 1998; Brumm and Todt, 2002), cats (Nonaka *et al.*, 1997), whales (Parks *et al.*, 2011), bats (Tressler and Smotherman, 2009), non-human primates (Sinnott *et al.*, 1975), and humans (Garnier *et al.*, 2010; Stowe and Golob, 2013). The presence of background noise sometimes affects not only vocal amplitude but also other vocal characteristics, such as fundamental frequency (F0) and duration (Brumm and Slabbekoorn, 2005), which were considered to be related to amplitude to some

extent, from the point of view of vocal mechanism. For example, in songbirds the amplitude and the F0 were positively correlated at the peripheral organ of vocalization, syrinx (Goller and Suthers, 1996). However, the mechanism of the noise-induced change of acoustic features has been poorly understood in humans, as well as in other animals. In order to understand the audio-vocal interaction, comparative ethological and neuroscientific studies are important (Brumm and Zollinger, 2011).

Songbirds learn species-specific songs as juveniles and vocalize complex songs (Soha and Marler, 2000). Their vocalizations are studied in detail by researchers from various fields, including ethology, neurobiology, and molecular biology (Bottjer and Johnson, 1997). The Bengalese finch (Lonchura striata var. domestica) is one of the model animals for the study of human vocalization (Bolhuis et al., 2010) because they use real-time auditory feedback information of the vocalization, as do humans (Okanoya and Yamaguchi, 1997). This species is also suitable for the study of audiovocal interaction (Dooling, 1980). Although Kobayasi and Okanoya (2003) reported only that the amplitude of their entire song, as root-mean-square (RMS) values, rose against background noise, in order to understand the audio-vocal interaction in detail, it is necessary to investigate how each distinct element (i.e., note) of the song can change according to the background noise.

In this paper, we present an accurate analysis of the Bengalese finch song, demonstrating how the amplitude and F0 of each note change against background noise, in order to understand the audio-vocal interaction. Instead of white noise, we used bandpass-filtered noises as the background

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noise, which allowed us to precisely analyze changes in each note by measuring acoustical features beyond the spectral range of the noise.

II. MATERIAL AND METHODS

Four types of noises were played back continually while Bengalese finches were recorded during a whole day. We examined how the amplitude and F0 of each note type changed by classifying the notes, calculating the F0 and amplitude of frequency components that were not masked by noise, and assessing changes in them in response to the noise presentation.

A. Subjects and recording setup

Thirteen adult male Bengalese finches were used in this experiment [Fig. 1(a)]. Eight of them, whose ages ranged from 212 to 1573 days post-hatch ($M \pm SD$ (standard deviation): 666.0 \pm 445.1 day), had been bred and maintained in the aviary at the University of Tokyo. The other five were known to be adult (>120 days), though their exact ages were unknown. The birds were housed under a 13:11-h light:dark cycle.

For the song recordings, a plastic birdcage (31 cm \times 16 cm \times 22 cm) was set in a soundproof chamber (58 cm \times 40 cm \times 37 cm), and an electric condenser microphone (PRO35, Audio-Technica, Japan) was placed 3 cm above the top of the cage. The song signals were digitally recorded through an audio interface (UA-22, Roland, Japan) at a 44.1kHz sampling rate and 16-bit resolution.

B. Noise stimuli

Four types of noise stimuli were alternatively presented to the birds during their song recordings [Fig. 1(b)]. Two were high-pass-filtered noise whose sound levels were either 60 dB or 70 dB ("H60" or "H70," respectively), while the other two were 60-dB and 70-dB low-pass-filtered noise ("L60" and "L70," respectively). We used these band-limited noises in order to analyze notes' frequency components that were outside of the spectra of the noises.

An A-weighted broadband noise was high-passed or lowpassed by Butterworth filters with a passband of 4.0-7.8 kHz ("H") or 0.2-4.0 kHz ("L"), using Adobe Audition software (Adobe System Corp., San Jose, CA; 80th order and 200-Hz transition band). The boundary frequency between H and L (4 kHz) was almost the midpoint of the audible range of finches and corresponds approximately to the peak of their hearing curve (Okanoya and Dooling, 1987). The sound pressure level of the filtered noise was adjusted to 60 dB(A)("60") or 70 dB(A) ("70"), as measured with a sound-level meter (NA-27, Rion, Japan) at the center of the perch in the chamber. The noises were played through the audio interface and a loudspeaker (MS101-III, YAMAHA, Japan), which was located at a distance of 18 cm from the microphone of the sound-level meter. With no sound playing through the speaker, the background sound level was $30.7 \, dB(A)$.

C. Experimental procedure

Undirected songs ("solo" songs without directing to female) of each male Bengalese finch were recorded with the bird left alone in the chamber. The bird was put into the cage in the evening of the day before the recording day, and its undirected songs were recorded during the entire next day from 8:00 a.m. to 5:20 p.m. The recording consisted of seven experimental cycles in a day in order to discriminate the noise-related changes from other spontaneous intraday fluctuations in song properties. The duration of each cycle was 80 min, during which the four types of noise were played for 10 min each at 20-min intervals [Fig. 1(c)]. The control condition, when the noises were not played, occurred for a total



ranges of two band noises used in the experiment drawn on song spectrograms. The lower band-limited noise (L noise), and the upper (H noise) had spectral ranges at 0.2-4.0 kHz and 4.0-7.8 kHz, respectively. (c) Schematic drawing of experimental procedure. Experiments consisted of seven experimental cycles, each of which had four times of 10-min playback of noise and four 10-min control conditions where no noise was presented. The order of four noise types was randomized within each cycle.

FIG. 1. (a) Example spectrogram of Bengalese finch's song. (b) Spectral

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of 40 min during every cycle. The order of the four noises was randomized for each bird, and the stimulus presentation was controlled with an original program written in the processing language.

D. Note classification and noise reduction

All the data recorded from each bird were tagged with the cycles and the five conditions (H60/H70/L60/L70/control). All the notes were initially segmented, detected, and classified using MATLAB software. Then, the frequency spectra of the noises were filtered and reduced in order to compare notes in the control conditions with those in the H and L conditions. Finally, the notes were detected and classified again.

The segmentation and detection were performed on the notes in the control condition by obtaining the amplitude envelope, thereby setting a threshold for the amplitude. In the detection procedure, notes that were much shorter (<20 ms) or much longer (>300 ms) and gaps that were much shorter (<5 ms) than usual were eliminated. Then, the notes were classified into note types represented with labels, using a linear support vector machine (SVM) multi-classifier algorithm with an acoustical feature space of 532 dimensions (Tachibana *et al.*, 2014). Notes in every first minute of the control condition of each cycle were labeled manually as the instruction data (with letters), and the rest of the notes in that condition were classified automatically.

Before the classification of notes in the H and L conditions, the spectra of the noise stimuli were reduced in all the recording data. The data recorded under the H (noise at 4.0-7.8 kHz) conditions were bandpass filtered at 0.2-3.2 kHz (Butterworth, 74th order, 200-Hz transition band) and the data of the L (noise at 0.2-4.0 kHz) conditions were bandpass filtered at 4.8-7.8 kHz (Butterworth, 80th order, 200-Hz transition band). The data from the control condition were also filtered in either of these two ways, to be compared with either the H or the L condition. The filtering procedure could slightly change the features because the duration of detected notes could be changed, although the influence of filtering was canceled out in comparisons between control and H/L conditions, since the same filter was applied in each case. After bandpass filtering, the notes in the control conditions, which were filtered in the two ways, were segmented, detected, and classified again, with the label information obtained before the filtering procedure. Using the notes in the control conditions of each cycle as the instruction data, all the notes of the noise conditions were classified and labeled using the linear SVM multi-classifier algorithm.

All the notes were classified into 13.5 ± 2.4 note types per bird. For each bird, 1–6 note types were selected that had clear and distinct frequency components and a successful classification, assessed by visually checking a severalminute excerpt of the song's spectrogram. Two of the birds rarely sang and classification was unsuccessful in another bird and, therefore, these three birds were removed from the analysis that follows. In total, 31 note types in the H conditions and 21 note types in the L conditions were obtained, each from nine birds.

E. Extraction of acoustic characteristics

The amplitude and F0 were calculated for each note. These were the power and the frequency, respectively, at the strongest component of the frequency spectrum of each note within a time window and frequency range that were defined before the calculation.

The specifics of the calculation were as follows. First, the average spectrogram of all the notes of the same note type was obtained. Then, the time window and the frequency range for each note type were determined by visual inspection of the averaged spectrogram. The length of each time window was 11.61 ms (512 samples). The excerpt of each note within the time window was converted into the frequency domain [fast Fourier transform (FFT) size: 8192], and the most intense component of the frequency was detected within the frequency range. Then, the five points consisting of the strongest frequency bin and four neighboring points were fitted by a parabolic curve using the leastsquares method. The amplitude and F0 were estimated using the power and the frequency at the apex of the fitted curve. If necessary in order to obtain the fundamental frequency, the frequency was divided by the harmonic number that was set before for each note type.

Outliers were removed for each cycle, each condition, and each note type as follows. First, notes that had obvious diversion of either amplitude or F0 were removed manually. Additionally, if there remained more than 100 notes in the subset after manual removal, notes whose acoustic characteristic was greater than the third quartile + 1.5 interquartile range (IQR) or less than the first quartile - 1.5 IQR of the subset were removed. This removal process excluded on average $6.09 \pm 6.54\%$ (H) and $5.57 \pm 5.00\%$ (L) of the samples per note type and, thus, we finally collected 1178 ± 715 (H) and 1124 ± 627 (L) samples per note type.

F. Assessment of changes in characteristics of the entire song

The changes in the characteristics of the entire song of each bird were calculated as follows. First, the characteristics under the noise conditions were standardized by dividing the means obtained for each note type by the control condition of the same cycle. Second, all the standardized values in all the cycles and note types were averaged into one mean value for each bird and each noise condition. The obtained mean values represented changes in the amplitude or F0 of the entire song for each bird. The amplitude and the F0 were converted to the logarithmic units of dB ($20 \times \log_{10}$ amplitude) and cents ($1200 \times \log_2$ frequency), respectively. After that, the values from all the birds were tested to determine whether they differed from zero (no changes) compared with the control condition, using the one-sample *t*-test (significant level $\alpha = 0.05$) with the Bonferroni correction for three multiple comparisons.

G. Assessment of changes in characteristics of each note

The changes in the characteristics of each note type were calculated as follows. First, the characteristics under all

the conditions were corrected for intraday changes. Second, the mean value of each characteristic was calculated for each note type and each condition for the whole day. After all the mean characteristics for every note type were converted to dB and cents, those in the noise conditions were checked to determine whether they differed from those in the control condition, using the Friedman test.

The correction for intraday changes, if any, in the characteristics was needed in order to compare the values between the conditions directly without standardizing them. Using the control condition, the amount of gradual change for each cycle was calculated as $\mu_{cycle} - \mu_{day}$ for each note type. Here, μ_{cycle} ("mean within a cycle") was the mean within the cycle and μ_{day} ("mean within a day") was the mean across all the cycles. Then, the correction was done as $x_{corr} = x - (\mu_{cycle} - \mu_{day})$, where x represents the value of the given acoustical characteristics of the note.

After the correction, the characteristics of all the notes in all the cycles were averaged for each note type and each condition, converted to the logarithmic units. Each note type, consequently, had the mean characteristics for each condition. Then, the Friedman test ($\alpha = 0.05$) and *post hoc* pairwise multiple comparison were performed for each characteristic in the H conditions and in the L conditions separately. The H and L conditions were not compared directly because the filtering processes in the analysis were different from each other.

III. RESULTS

We examined how the amplitude and F0 of each note changed in the Bengalese finch songs against background noise, in order to investigate the audio-vocal interaction in detail. The amount of change shown in the results was obtained by subtracting the acoustic features in the control condition from those in each of the noise conditions (H60, H70, L60, L70). After the calculation procedure, 31 note types in the H conditions and 21 note types in the L conditions were analyzed. The F0s of all the note types analyzed ranged 0.63-3.26 kHz ($M \pm$ SD: 2.08 ± 0.65 kHz) in the H conditions, and 1.69-3.67 kHz (2.69 ± 0.56 kHz) in the L conditions.

The background amplitudes of the silent parts (without any songs or bird's motion noises) were compared between the noise and the control conditions in order to confirm that changes in amplitude were not caused by noise stimuli themselves. One-second excerption of recording when the bird kept quiet in each condition was picked up randomly for each bird, the RMS of which was calculated after the noise reduction procedure. As a result, the background amplitudes of the silent parts did not differ either among the H conditions (control: -66.51 ± 1.04 dB, H60: -66.48 ± 1.03 dB, H70: -66.29 ± 0.84 dB) or among the L conditions (control, -77.26 ± 0.72 dB, L60: -77.33 ± 0.80 dB, L70: -77.28 ± 0.72 dB).

A. Changes in characteristics of the entire song

The mean amplitude of each bird's song increased slightly [Fig. 2(a)]. The changes were from -0.52 to +0.67 dB $(0.38 \pm 0.25$ dB) in the H60 condition, from +0.04 to

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+ 0.88 dB (0.42 ± 0.30 dB) in the H70 condition, from -0.15 to +1.21 dB (0.42 ± 0.41 dB) in the L60 condition, and from -0.52 to + 1.79 dB (0.46 ± 0.76 dB) in the L70 condition. In the H60, H70, and L60 conditions the amplitude increased with statistical significance [one-sample *t*-test with the Bonferroni correction, N = 9 birds, degree of freedom (df) = 8. H60: t = 4.57, p = 0.004; H70: t = 4.25, p = 0.006; L60: t = 3.08, p = 0.030; L70: t = 1.84, p = 0.206].

On the other hand, there was less of an increase observed in the F0, although the mean value did increase slightly [Fig. 2(b)]. The changes were from -2.39 to +12.9 cents (4.15 ± 4.75 cents), from -6.71 to +10.44 cents (3.30 ± 5.25 cents), from -16.90 to +9.98 cents (2.43 ± 7.82 cents), and from -21.85 to +21.67 cents (1.38 ± 12.41 cents) in the H60, H70, L60, and L70 conditions, respectively. Here, 100 cents is a semitone. There was a tendency of increase only in the H60 condition (one-sample *t*-test with the Bonferroni correction, N=9 birds, df = 8. H60: t=2.62, p=0.061; H70: t=1.89, p=0.192; L60: t=0.94, p=0.748; L70: t=0.33, p=1.000).

B. Changes in characteristics of each note

As in the entire song, the amplitude of each song element likewise increased [Fig. 3(a)]. The changes in the H60 and H70 conditions were from -0.51 to +1.48 dB (0.35 \pm 0.41 dB) and from -0.82 to +1.50 dB (0.31 ± 0.52 dB), while those in the L60 and L70 conditions were from -0.39 to +1.50 dB (0.31 ± 0.58 dB) and from -1.72 to +3.19 dB (0.45 ± 1.06 dB), respectively. The effect of the H noises was significant (Friedman test; H: N = 31 notes, df = 2, $\chi^2 = 17.48$, p < 0.001; L: N = 21 notes, df = 2, $\chi^2 = 2.95$, p = 0.229). Conducting *post hoc* pairwise comparison, the increases in the H60 and H70 conditions were significant against the control condition (control vs H60: p < 0.001; control vs H70: p = 0.991).

The changes in F0 [Fig. 3(b)] were as follows: from -8.94 to +21.62 cents $(3.78 \pm 7.24$ cents) in the H60 condition, from -14.75 to +21.77 cents $(2.24 \pm 8.88$ cents) in the H70 condition, from -20.02 to +15.21 cents (0.46 ± 9.90) cents) in the L60 condition, and from -24.26 to +27.28 cents $(1.50 \pm 14.41$ cents) in the L70 condition. By the statistical test, the effect of the H noises was shown to be significant (Friedman test; H: N=31 notes, df = 2, $\chi^2 = 6.26$, p = 0.044; L: N = 21 notes, df = 2, $\chi^2 = 1.14$, p = 0.565). Conducting *post hoc* pairwise comparison, the F0 in the H60 condition increased against the control condition with statistical significance (control vs H60: p = 0.042; control vs H70: p = 0.177; H60 vs H70: p = 0.801).

IV. DISCUSSION

We measured the changes in the amplitude and F0 of the Bengalese finch songs in response to background noises. We used bandpass-filtered noises to precisely analyze the acoustic characteristics of notes. Our results show that the amplitude increased significantly in the H conditions and that the F0 increased in the H60 condition. The results for the entire song's comparison (Fig. 2) were similar to those for each note's comparison (Fig. 3).



FIG. 2. (Color online) Changes in amplitude (a) and fundamental frequency (F0) (b) for all the birds under the four noise presentations. Each dot shows the change in the given characteristics for the entire song of each bird compared with the control condition. Each dot color represents a different bird. A semitone is 100 cents. A one-sample *t*-test was performed for each characteristic and the H or L condition (Bonferroni-corrected). (a) Statistically significant changes were observed in the H60 (p < 0.01), H70 (p < 0.01), and L60 (p < 0.05) conditions, and (b) tendency to increase was observed in the H60 condition (p < 0.1).

A. Amplitude changes

From the increases in amplitude under the H conditions, it can be seen that the Lombard effect occurred in each note of the Bengalese finch songs, contributing to the resulting change in the entire song. This suggests that they increase the amplitude of every note, but not just specific types of notes, in response to specific noise. In previous studies, the Lombard effect has been observed to improve the signal-tonoise ratio (SNR; Brumm and Zollinger, 2011). The increase shown in the present experiment could have the function of improving the intelligibility (i.e., SNR) for the bird itself, as well as for other recipient birds, regarding that Bengalese finches need the auditory feedback of their own songs while singing in real time (Okanoya and Yamaguchi, 1997). The increase observed in our experiment ($\sim 2 dB$) is not so great as the increases in amplitude reported in past studies on other birds' vocalization (Cynx et al., 1998; Kobayasi and Okanoya, 2003; Pytte et al., 2003). This difference might be because we used bandpass-filtered noise as stimulus, which had a narrower frequency band than the white noise used in the past experiments. In spite of the increase under the L60 condition, there were less prominent effects in the L70 condition. The L70 condition produced larger variability in both the amplitude and F0 changes. This anomaly might be caused by spectral band-specific differences in bird's auditory sensitivity, though further investigations on noise bandspecific responses will be required in future studies.

B. F0 changes

The F0 change found was not as clear as that for the amplitude, although the statistical test showed a significant increase under the H60 condition [Fig. 3(b)]. This change reflected individual differences, rather than note-specific differences of the original values of the amplitude and F0. The different results between the amplitude and F0 suggest that the relationship between them in the overall control system of vocalization would not be so simple that it could be predicted by the peripheral mechanism of vocalization, which showed positive correlation between them (Goller and Suthers, 1996). Also, there was no significant correlation between the original F0 and the change of the F0 for each note type, suggesting there were no tendencies of the F0 change specific to note types (Pearson's correlation coefficient. H60: r = 0.290, p = 0.114; H70: r = -0.081, p = 0.664; L60: r = 0.085, p = 0.715; L70: r = -0.034, p = 0.883). Rather, one bird (bf01) lowered the F0 of almost



FIG. 3. (Color online) Changes in (a) amplitude and (b) F0 for all the notes under four noise presentations. Each dot shows the change in the given characteristic for each note type compared with the control condition. Each dot color represents a different bird. A Friedman test was done for each characteristic, and the H or L conditions. (a) The increase in the H60 (p < 0.01) and H70 (p < 0.01) conditions were statistically significant against the control condition and (b) the F0 in the H60 condition (p < 0.05) increased against the control condition with statistical significance.

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all its notes under all the conditions [Figs. 2(b) and 3(b)]. A statistical analysis without the data from this bird showed significant increases in F0 in the H conditions and a tendency of increase in the L conditions (Friedman test; H: N = 25notes, p = 0.001, df = 2, $\chi^2 = 13.52$; L: N = 17 notes, p = 0.056, df = 2, $\gamma^2 = 5.76$). The post hoc pairwise comparison showed that the F0 increased with statistical significance in the H60 and H70 conditions, compared with the control condition (control vs H60: p = 0.005; control vs H70: p = 0.003; H60 vs H70: p = 0.989). These results suggested the F0 change might be more variable between individuals rather than between note types, although there was no tendency of change according to age. Such individual variability has also been reported in a human vocalization study. Some individuals tended to increase almost all their F1 frequencies on vowel formants, while another individual showed increases and decreases in F1 frequencies of utterances according to words, against the presence of background noise (Van Summers et al., 1988). As in the human study, Bengalese finches may have some individual-specific tendencies in their F0 changes. This similarity suggests that these two species might have similar mechanisms of F0 control in vocalization with auditory feedback. Additionally, similar to the results found for the amplitude, the SDs of the changes in F0 under the L70 condition were much larger than those under the other conditions.

C. Difference in change patterns between H and L conditions

The difference in the changes in amplitude and F0 against noise of the different frequencies might result from the factors below. First, it could be affected by differential importance of the respective spectral regions in recognizing each note. In humans, the Lombard effect is known to occur when the noise frequency is superposed on the spectral range that is important for the distinction of vowels in speech (Stowe and Golob, 2013). Although all the F0s of the notes in our experiment were under 4 kHz (within the L noise frequency), Bengalese finches might rely more on the spectral range of the H noise than that of the L noise in order to recognize notes. Second, there was individual variability in the changes in acoustic characteristics, as suggested by the F0 data. It has been also reported that there is variation within an individual in frequency changes in human vocalizations (Van Summers et al., 1988). The within-individual variation indicates the different types of change between different note types, probably resulting from the physical characteristics of the vocalization organs. The difference between the changes under the H and L conditions could arise from a combination of these causes. Finally, it should be noted that the calculation method used in this experiment would have a limitation to incorporate all the changes in each note because the calculation depended on the restricted frequency spectrum and time window. Therefore, the amplitude might be affected by changes in the frequency envelope of the notes, and both characteristics might be influenced by changes over time, if any.

In any case above, the results in the present study suggested the vocal control mechanism on which the auditory feedback is based has nonuniform, complex effects for individual note productions. For future research, it is important to investigate the neural and physical mechanisms of how to control the acoustic characteristics at the note level. Furthermore, the individual variation reported here should be investigated in detail in order to understand the neural mechanism of the control of acoustic characteristics in vocalization. It would be also interesting to investigate whether there is any aftereffect on vocalization induced by noise presentation, whereas the present study focused only on transient effects.

We have confirmed that the Lombard effect occurs in each note of Bengalese finch song, and have also shown that there might be a variation of the F0 change, both between and within individuals. In future research, it will be important to segregate the possible factors that could result in the different changes in the acoustic characteristics against different noise presentations. In particular, the individual variation, which has also been reported in human studies, should be one key factor in understanding noise-induced vocal changes. A detailed investigation into this would shed light on the neural mechanisms of the control of acoustic characteristics and the audio-vocal interaction in Bengalese finches, which would contribute to the understanding of these factors in humans.

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- Bolhuis, J. J., Okanoya, K., and Scharff, C. (2010). "Twitter evolution: Converging mechanisms in birdsong and human speech," Nat. Rev. Neurosci. 11(11), 747–759.
- Bottjer, S. W., and Johnson, F. (**1997**). "Circuits, hormones, and learning: Vocal behavior in songbirds," J. Neurobiol. **33**(5), 602–618.
- Brumm, H., and Slabbekoorn, H. (2005). "Acoustic communication in noise," Adv. Study Behav. 35, 151–209.
- Brumm, H., and Todt, D. (2002). "Noise-dependent song amplitude regulation in a territorial songbird," Anim. Behav. 63(5), 891–897.
- Brumm, H., and Zollinger, S. A. (2011). "The evolution of the Lombard effect: 100 years of psychoacoustic research," Behaviour 148(11–13), 1173–1198.
- Cynx, J., Lewis, R., Tavel, B., and Tse, H. (1998). "Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*," Anim. Behav. 56(1), 107–113.
- Dooling, R. J. (1980). "Behavior and psychophysics of hearing in birds," in *Comparative Studies of Hearing in Vertebrates* (Springer, Berlin), pp. 261–288.
- Garnier, M., Henrich, N., and Dubois, D. (2010). "Influence of sound immersion and communicative interaction on the Lombard effect," J. Speech Lang. Hear. Res. 53(3), 588–608.
- Goller, F., and Suthers, R. A. (1996). "Role of syringeal muscles in controlling the phonology of bird song," J. Neurophysiol. 76(1), 287–300.

- Jürgens, U. (2009). "The neural control of vocalization in mammals: A review," J. Voice 23(1), 1–10.
- Kao, M. H., Doupe, A. J., and Brainard, M. S. (2005). "Contributions of an avian basal ganglia–forebrain circuit to real-time modulation of song," Nature 433(7026), 638–643.
- Kobayasi, K. I., and Okanoya, K. (2003). "Context-dependent song amplitude control in Bengalese finches," Neuroreport 14(3), 521–524.
- Lombard, E. (1911). "Le signe de l'elevation de la voix" ("The sign of the elevation of the voice"), Ann. Maladies Oreille, Larynx, Nez, Pharynx 37(101–119), 25.
- Manabe, K., Sadr, E. I., and Dooling, R. J. (1998). "Control of vocal intensity in budgerigars (*Melopsittacus undulatus*): Differential reinforcement of vocal intensity and the Lombard effect," J. Acoust. Soc. Am. 103(2), 1190–1198.
- Nonaka, S., Takahashi, R., Enomoto, K., Katada, A., and Unno, T. (1997). "Lombard reflex during PAG-induced vocalization in decerebrate cats," Neurosci. Res. 29(4), 283–289.
- Nottebohm, F. (1972). "The origins of vocal learning," Am. Nat. 116-140.
- Okanoya, K., and Dooling, R. J. (1987). "Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds," J. Comp. Psychol. 101(1), 7.
- Okanoya, K., and Yamaguchi, A. (1997). "Adult bengalese finches (*Lonchura striata* var. *domestica*) require real-time auditory feedback to produce normal song syntax," J. Neurobiol. 33(4), 343–356.
- Parks, S. E., Johnson, M., Nowacek, D., and Tyack, P. L. (2011). "Individual right whales call louder in increased environmental noise," Biol. Lett. 7(1), 33–35.

- Purcell, D. W., and Munhall, K. G. (2006). "Compensation following realtime manipulation of formants in isolated vowels," J. Acoust. Soc. Am. 119(4), 2288–2297.
- Pytte, C. L., Rusch, K. M., and Ficken, M. S. (2003). "Regulation of vocal amplitude by the blue-throated hummingbird, *Lampornis clemenciae*," Anim. Behav. 66(4), 703–710.
- Seyfarth, R. M., Cheney, D. L., and Marler, P. (1980). "Vervet monkey alarm calls: Semantic communication in a free-ranging primate," Anim. Behav. 28(4), 1070–1094.
- Sinnott, J. M., Stebbins, W. C., and Moody, D. B. (1975). "Regulation of voice amplitude by the monkey," J. Acoust. Soc. Am. 58(2), 412–414.
- Soha, J. A., and Marler, P. (2000). "A species-specific acoustic cue for selective song learning in the white-crowned sparrow," Anim. Behav. 60(3), 297–306.
- Stowe, L. M., and Golob, E. J. (2013). "Evidence that the Lombard effect is frequency-specific in humans," J. Acoust. Soc. Am. 134(1), 640–647.
- Tachibana, R. O., Oosugi, N., and Okanoya, K. (2014). "Semi-automatic classification of birdsong elements using a linear support vector machine," PLoS One 9(3), e92584.
- Tressler, J., and Smotherman, M. S. (2009). "Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats," J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol. 195(10), 923–934.
- Van Summers, W., Pisoni, D. B., Bernacki, R. H., Pedlow, R. I., and Stokes, M. A. (1988). "Effects of noise on speech production: Acoustic and perceptual analyses," J. Acoust. Soc. Am. 84(3), 917–928.

